

PRELIMINARY REPORT ON A NEW ANKYLOSAUR FROM THE EARLY
CRETACEOUS OF QUEENSLAND, AUSTRALIA

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The skeleton of a small ankylosaur, referred to the genus *Minmi* (Molnar 1980), was recovered from the Albian Allaru Mudstone of north-central Queensland. The specimen shows most of the contacts between the cranial bones and preserves most of the dorsal armor in place. Unusual features include an apparently very large inferior process of the premaxilla, thin ventral sheets of the nasals, an apparently rod-like, vertical lachrymal, and a pronounced coronoid process on the mandible. The ilium is joined to two sacrals by a broad 'bridge' of bone. The skeleton is thought to derive from a mature or almost mature individual, and may have been mummified before burial. □ *Early Cretaceous, ankylosaur, Australia, taphonomy.*

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The most complete dinosaurian specimen yet found in Australia was discovered by Mr Ian Ievers in north-central Queensland in November 1989. While resting on an outcrop of limestone concretions, he noticed fossil bone in them. He then contacted the Queensland Museum and the specimen was collected in January 1990. Mr Ievers subsequently located further blocks, with parts of the neck and shoulder girdle, which he kindly forwarded to the museum.

This specimen represents the most complete dinosaurian material yet found in eastern Gondwanaland (Australia and Antarctica) and one of the most complete Early Cretaceous ankylosaurs. In addition it is one of the few ankylosaurs to clearly show the contacts between the cranial bones and the disposition of the dorsal dermal armor, almost all of which seemingly remains in place.

Because both preparation and study have yet to be completed, this account will necessarily emphasise the features that have been studied, especially the dermal armor and cranial morphology. More cursory comments on postcranial elements are also included. A complete description, together with an analysis of the phylogenetic relationships and description of another recently-discovered thyreophore skeleton (probably conspecific), is contemplated for the near future. Popular discussions of the specimen have been published in Japan (Molnar, 1994) and Australia (Molnar, 1991a, 1991b), and color photos of the reassembled specimen have been published in popular books (Lambert, 1993; Lambert & Bunting, 1995; Tomida & Sato, 1995).

Collection designations. AM, Australian Museum, Sydney; QM, Queensland Museum, Brisbane.

Abbreviations. b, sheet of bone linking scurum and ilia; Bo, basioccipital; D, ossification of dermal armor; Dy, dentary; Eo, exoccipital (paroccipital process); F, frontals; fm, foramen magnum; J, jugal; L, (presumed) lachrymal; lf, left femur; lh, left humerus; li, left ilium; lu, left antibrachium; m, unremoved matrix; Mx, maxilla; N, nasals; n, neural spines; o, orbit; P, parietals; Pf, prefrontal; Pm, premaxilla; Po, postorbital; Pof, postfrontal; Pt, pterygoid; Q, quadrate; Qj, quadratojugal; R, nasal passage; ri, right ilium; S, presumed sinus chamber; s, skull; So, supraorbital; Soc, (presumed) suraoccipital; Sq, squamosal; 'Sq', squamosal, postfrontal & postorbital; sr, sacral ribs; stf, supratemporal fenestra; t, transverse processes.

OCCURRENCE AND STRATIGRAPHY

The specimen (QM F18101) was found on a low ridge in open country south of the Flinders River on Marathon Station, east of Richmond, north-central Queensland. The bones were partially enclosed in silty buff-grey micrite concretions. These concretions derive from weathering of the Albian Allaru Mudstone, which consists of mudstones and siltstones, often calcareous, deposited in the inland sea.

The carbonate was deposited immediately around the skeleton, with no large masses free from bone. This suggests that the nodule may originally (prior to its weathering in the soil) have roughly preserved the body outline of the carcass.

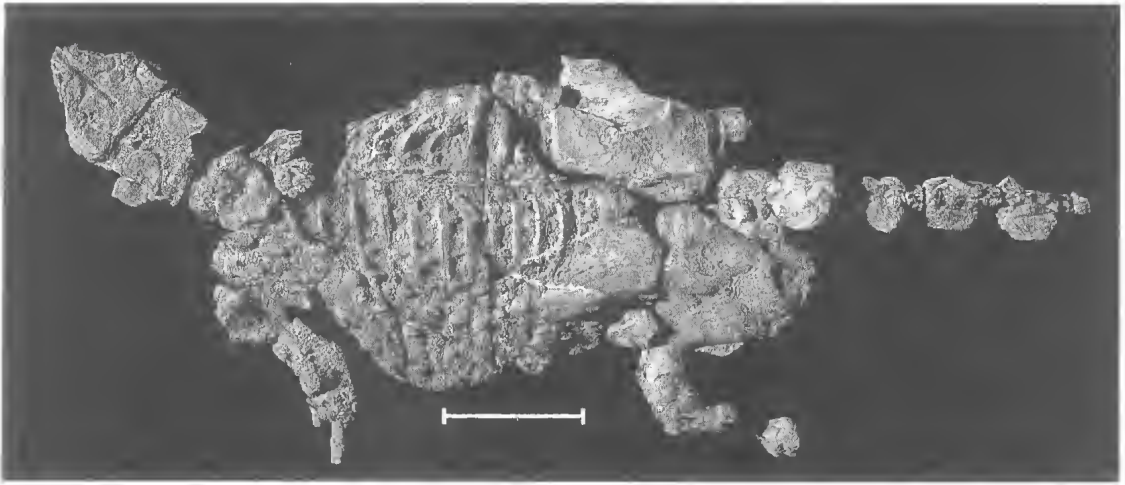


FIG. 1. Reassembled skeleton of the ankylosaur, *Minmi* sp. (QM F18101), from north-central Queensland. This photo was taken prior to beginning preparation. Scale = 250mm.

The ribs, dorsal armor and tips of the neural spines were exposed on the lower surfaces of the blocks almost as though artificially prepared, but the ilia were almost completely covered by carbonate. The remaining elements, especially the distal limb pieces, were found either in small blocks of carbonate or as isolated bones in the soil.

The skeleton was intimately associated with abundant plates of *Inoceramus* shell, a few *Echinorhinus* teeth and part of one small, incomplete — and unfortunately indeterminate — ammonite. The Allaru on 'Marathon' has also yielded large teleosts, ichthyosaurs (Etheridge, 1888) and a nearly complete small sauropterygian, as well as marine invertebrates, but no other terrestrial forms. Nonmarine tetrapods from the Allaru elsewhere in central Queensland include *Muttaborrasaurus* sp. (Molnar, this volume) and a pterosaur. Six other specimens represent armored dinosaurs, probably ankylosaurs, all but one of which are fragmentary: they will not be described here.

IDENTIFICATION

Only a single armored dinosaur, *Minmi paravertebra* (Molnar, 1980), is known from Australia. This specimen matches the holotype *M. paravertebra* in the possession of paravertebrae, ossified aponeuroses and tendons along the dorsal vertebral column. However the type of *M. paravertebra* derives from the Aptian Bungil Fm. whereas this specimen is from the Albian. Since study of the new material is not yet com-

plete, and there may be differences of form in the ribs, the question of its specific allocation remains open. Furthermore the type material was too incomplete for a phylogenetic analysis, although the possession of paravertebrae is an autapomorphy for the genus (cf. Molnar, 1980). Hence the 'Marathon' specimen is herein designated *Minmi* sp. Pending the planned phylogenetic analysis the genus *Minmi* is presumed to belong to the Ankylosauria, but is not allocated to a family.

Only five Cretaceous thyreophores are known from the southern hemisphere outside Australia (cf. Molnar & Frey, 1987). Ankylosaurian material has recently been described from Upper Cretaceous beds in Antarctica (Gasparini et al., 1987; Olivero et al., 1991; Gasparini et al., this volume), New Zealand (Molnar & Wiffen, 1994), Argentina (Salgado & Coria, in press) and India (Chatterjee & Rudra, this volume). A stegosaur, *Dravidosaurus blanfordi*, has been reported from the Coniacian of India (Yadagiri & Ayyasami, 1979), the only stegosaur described from the Late Cretaceous. All of these are represented by substantially less complete specimens than that from 'Marathon'. Isolated ankylosaur elements have also been found in the Lower Cretaceous sediments of Victoria (Rich & V.-Rich, 1994).

DISPOSITION OF SKELETON

Since this is only a preliminary description of the skeleton, the completeness and condition of the specimen when collected are presented here separately from the description. The specimen

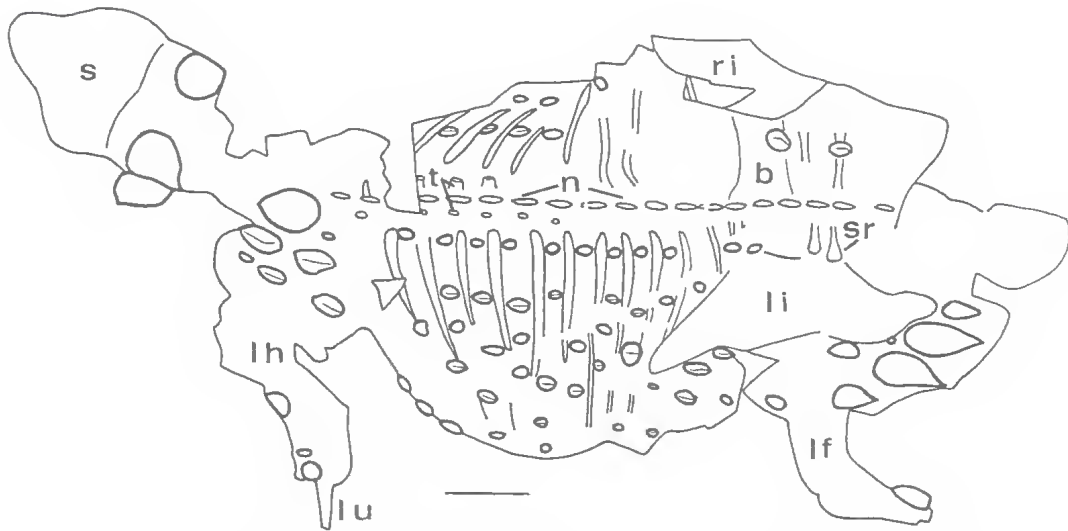


FIG. 2. The pattern of dorsal armor of *Minmi* sp. (QM F18101). Elements of the armor are shown in heavy outline, and endoskeletal elements (skull roof, tips of neural spines & transverse processes, dorsal & sacral ribs and ilia) are in light outline. Scale = 100mm.

includes most of the skull and the articulated axial skeleton back to the proximal tail, to probably the ninth caudal (Figs 1, 2). The arches of some vertebrae have been crushed. The neural arch of the axis was found isolated in the soil about a metre away from the block enclosing the skull and anterior cervicals. The more distal part of the tail was not found and the distal parts of both left limbs are also missing. The left shoulder girdle seems complete. The coracoids are not fused to the scapulae, and were displaced. The left humerus is almost complete and the proximal parts of both left radius and ulna are present. The left ilium is nearly complete, and the proximal halves of both ischium and pubis are also present on that side. Much of the right pelvis, however, has been lost. Both femora are essentially complete, but weathered, as are the crural elements. Only a few disarticulated manual and pedal elements were found, although the right manus may be embedded beneath the rib cage.

The specimen was upside down when excavated, except perhaps for the block containing the skull which had been uncovered before our arrival. The neural canal of one vertebra (enclosed in a small block of carbonate) contains sediment (with embedded dermal ossicles) at the top and white calcite crystals below clearly indicating the inverted position of the trunk in the ground.

When reassembled, the vertebral column is straight, except for the cervical column near the skull which inclines to the right at about 20° (Fig. 1). The base of the tail extends straight out posteriorly from the trunk and the pieces of the more distal part of the tail fit together to also give a straight column. The ribs on the left side have been flattened and so have lost their natural curvature, but the ribs on the right — except for those just in front of the pelvis — have been rotated backwards. The right ilium has apparently become separated from the sacrum and displaced forward and laterally. Both left fore and hind limbs extend laterally horizontally from the trunk, but both right limbs are folded across the belly. Both forelimbs are flexed at the elbow and both hindlimbs at the knee. The left femur is in situ in the acetabulum but projects horizontally, parallel to the top of the ilium. The trunk gives the impression of having collapsed to lay flat on the substrate.

MATURITY

Recently there has been much emphasis (e.g., Rowe & Gauthier, 1990) on using adult characters (in the sense of skeletal maturity) in phylogenetic classification and the unusual features of this specimen raise the question of whether or not it was mature, or nearly so. This skeleton was probably 2.5–3.5m long when com-

plete. This is a small ankylosaur (cf. Coombs & Maryanska, 1990): does it represent a small adult or an immature individual? All known early ankylosaurs (*Dracopelta*, *Priodontognathus*, *Sarcolestes* and *Tianchiasaurus*) are small, as are later, insular ankylosaurs such as *Struthiosaurus*. *Minmi* is a relatively early ankylosaur and, in addition, may have evolved on the east Queensland island of the Aptian (Dettmann et al., 1992). The holotype specimen of *Minmi paravertebra* was found in Aptian marine sediments (Bungil Fm.) near this island (Molnar, 1980) and probably derived from there (Fig. 3). If the lineage evolved there a small adult body size is plausible. Late Cretaceous European insular ankylosaurs (*Struthiosaurus*) are of about the same size as the holotype and the 'Marathon' animal, and notably smaller than those from western North America and central Asia.

Some features — absence of fusion of the cranial elements, absence of fusion of the scapulae and coracoids, absence of fusion of the pelvic elements — in addition to its small size, suggest that it was immature at death. But there are also reasons to suggest that was mature or nearly so. There are five other specimens from Queensland certainly or plausibly referred to the genus *Minmi*: QM F33565 and F33566 (probably deriving from a single individual and so considered here), AM F35259, QM F33286, QM F10329 (the holotype) and an unregistered specimen that will probably be housed at the Australian Museum. All of these, except the first which is also the most different morphologically and hence possibly represents a distinct taxon, are within 10% of the linear dimensions of the 'Marathon' skeleton. Ignoring the first specimen would suggest that all known specimens of Queensland ankylosaurs are mature but small, but including it indicates that five of six are immature, if the 'Marathon' skeleton is from an immature individual. It seems *prima facie* unlikely that of six specimens that were, judging from their geographical distribution, probably drawn from different populations, all but one would represent immature individuals at the same stage of growth. Nonetheless this is not impossible, especially as Horner (1979) pointed out that most occurrences of dinosaurs in marine beds are of immature individuals.

Although the junctions between the cranial bones generally are not fused both frontals and parietals are fused along the midline, and the contacts in braincase are fused. Fusion of the cranial elements is thought to be a marker of

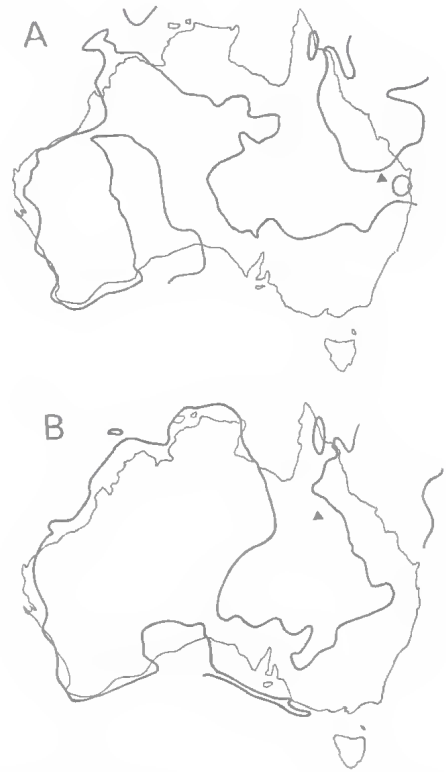


FIG. 3. Shorelines of Australia during the ages when *Minmi* lived, A, Aptian, B, Albian. Heavy lines mark contemporaneous shorelines, light lines modern shorelines. The triangles indicate the localities of *Minmi paravertebra* (A) and *Minmi* sp. (B). Both specimens probably drifted from the eastern Queensland landmass, which in the Aptian was a set of islands and in the Albian a peninsula. (Redrawn from Dettmann et al., 1992)

adulthood in ankylosaurs (Coombs & Maryanska, 1990), but lack of fusion is also the plesiomorphic state and cranial fusion may have developed only in later ankylosaurs. The maxilla of *Priodontognathus*, probably early Late Jurassic in age, shows no indication of having been fused to the other cranial bones (Galton, 1980). In the 'Marathon' specimen the coracoids are not fused to the scapulae. This lack of fusion is not considered a juvenile character by Coombs & Maryanska (1990) and some ankylosaurs lack fused scapulocoracoids as adults (Carpenter, 1990; Pereda-S., 1994).

Currie (pers. comm., 1991) observed that clearly juvenile *Pinacosaurus* have only ossicles making up the armor of the trunk. In the 'Marathon' *Minmi* the trunk armor comprises

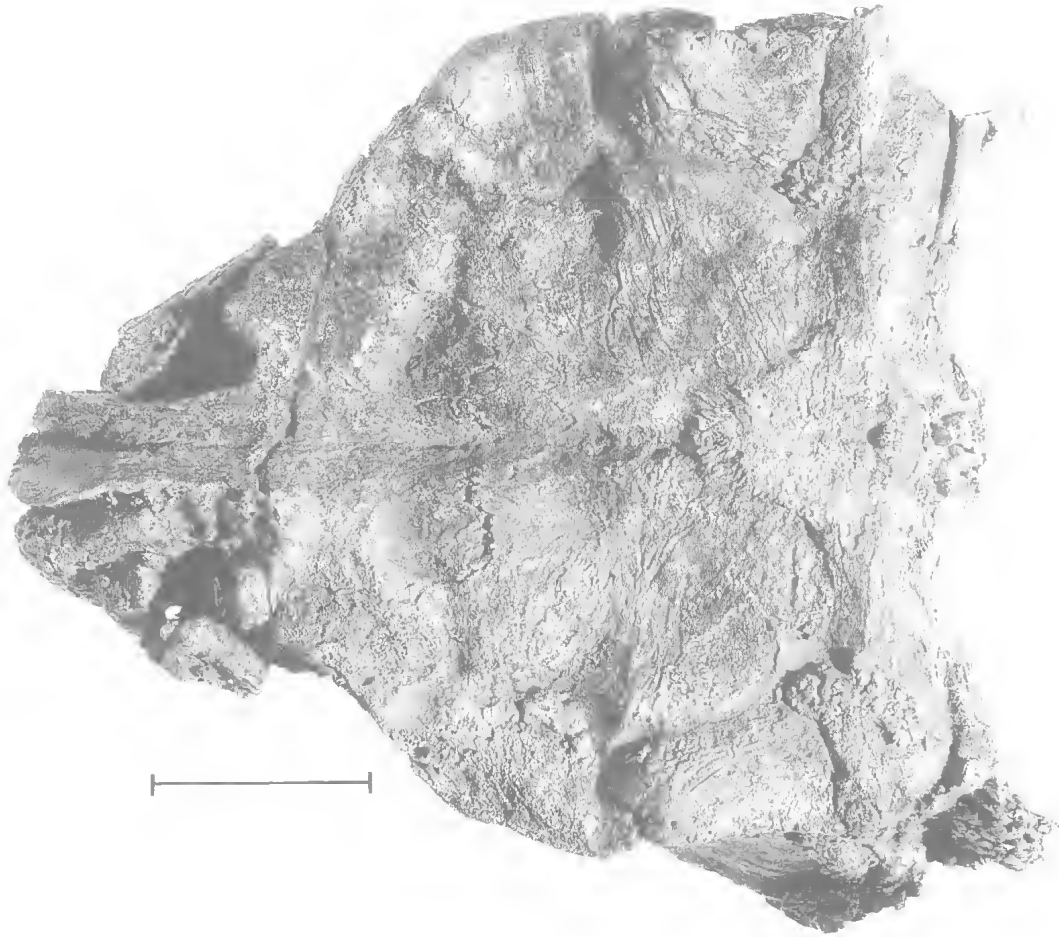


FIG. 4. Skull, in dorsal view, of *Minmi* sp. (QM F18101). Anterior is to the left. Elements of the dermal armor remain in the narial region and behind the quadrate. Scale = 50mm.

both ossicles and scutes, suggesting it was adult, or nearly so.

Thus although there are some grounds (contra Molnar, 1994) to think this specimen is a juvenile, these are not entirely compelling and it may simply be plesiomorphic. Tentatively the 'Marathon' specimen is best regarded as representing an almost mature, or newly mature, individual.

DISPOSITION OF ARMOR

Armor is present across the dorsum of the neck and trunk, as well as on the tail and limbs (Fig. 2). Several kinds of dermal elements are present: large nuchal, scapular, pelvic, appendicular and caudal scutes; small dorsal scutes; ossicles; and (probably) triangular caudal plates.

The broadly oval nuchal scutes are larger (to 13cm wide x 9cm long) than any of the dorsal scutes, and comparable in size to the pelvic scutes and caudal plates. Four (three of which are preserved) form an incomplete transverse band just behind the skull. The pair on either side are in contact (preserved on the left), but the medial of each pair are separated by a gap of 5.5cm. Behind this is a suite of one large (9.5 x 7.5cm) three medium (c. 5.5 x 3cm) and two small scutes (c. 2 x 1.5cm) arranged with the large one medially placed and the others spread laterally over the shoulder region. These shoulder scutes, like those of the back, are roughly oval with a low longitudinal keel and aligned parasagittally. They are preserved only on the left side.

The smaller scutes of the back are arranged linearly, at least towards the midline. A row of at

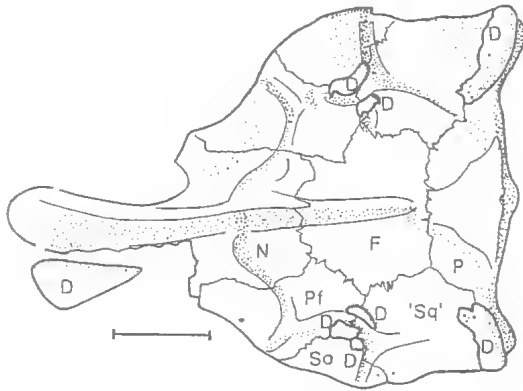


FIG. 5. Skull, in dorsal view, of *Minmi* sp. (QM F18101). Anterior is to the left. Occipital face not shown. The element on the left side of the nasals is a large piece of dermal armor placed in what is thought to be its proper position. Abbreviations given in text. Scale = 50mm.

least ten lay to either side of the vertebral column, extending from the base of the neck at least to the pelvic region. Further laterally, the arrangement is more haphazard, although this may arise from post-mortem disturbance. In all cases the scutes are placed between the ribs. The arrangement at the shoulder may be an extension of that of the back, but this is not clear. Unlike the shoulder scutes, on the back the lateral scutes are slightly larger than the medial.

Along the lateral side of the left ilium is a row of three large flat plates (to 10.5 x 7cm). Basically oval in form, they come to a sharp point posteriorly, and so look like tear-drops. Three of these are preserved, arranged sequentially along the posterior portion of the lateral margin of the ilium and curving around behind it. All except the last are displaced from the ilium, with but a few

medium or small scutes in the intervening region. Unfortunately, because this part of the specimen is almost completely flattened it is not clear whether these plates lay flush with the skin, or if the posterior points projected outwards above the hind limb.

The neck, back and limbs were probably completely covered by small ossicles embedded in the skin. Layers of ossicles are also found ventral to the vertebrae and ribs, in what was the body cavity. This suggests that like the holotype of *M. paravertebra*, the belly was also covered by a chain-mail of these ossicles. Some of the scutes, particularly those of the shoulder region, have the appearance of having been formed from — or at least augmented by — the accretion of ossicles.

The ossicles are rectangular to trapezoidal in outline and seem have two forms. One is convex with faint concentric ridges or striae, and the other an almost stellate form of sharp interconnecting ridges surrounding distinct pockets. Examination of ossicles freed during preparation, however suggests that there is only a single form. Presumably the 'stellate' face was directed externally and the convex, pillow-like face internally. The appearance of both forms in the armor preserved in place suggests that some have become inverted without having been displaced. Unbroken ossicles measure about 4 x 6mm.

The tail bore at least two kinds of armor. A row of two or three large, smooth triangular plates are preserved along one side of the tail. Their orientation is unclear. As preserved, they project ventrolaterally, but all are broken at their bases, as if they had been forced downwards into this position during preservation. In addition, there are keeled, pitted, roughly rectangular scutes, each slightly less than half as long as the triangular plates. Again their arrangement is not

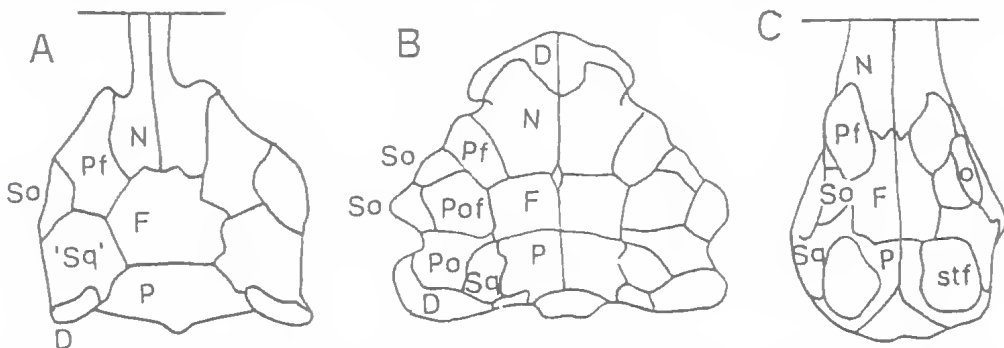


FIG. 6. Pattern of cranial elements in dorsal view for A, *Minmi* sp. B, *Pinacosaurus grangeri*; and C, *Scelidosaurus harrisonii*. Not to scale (*Pinacosaurus* after Maryanska (1977), *Scelidosaurus* after Coombs, et al. (1990)).

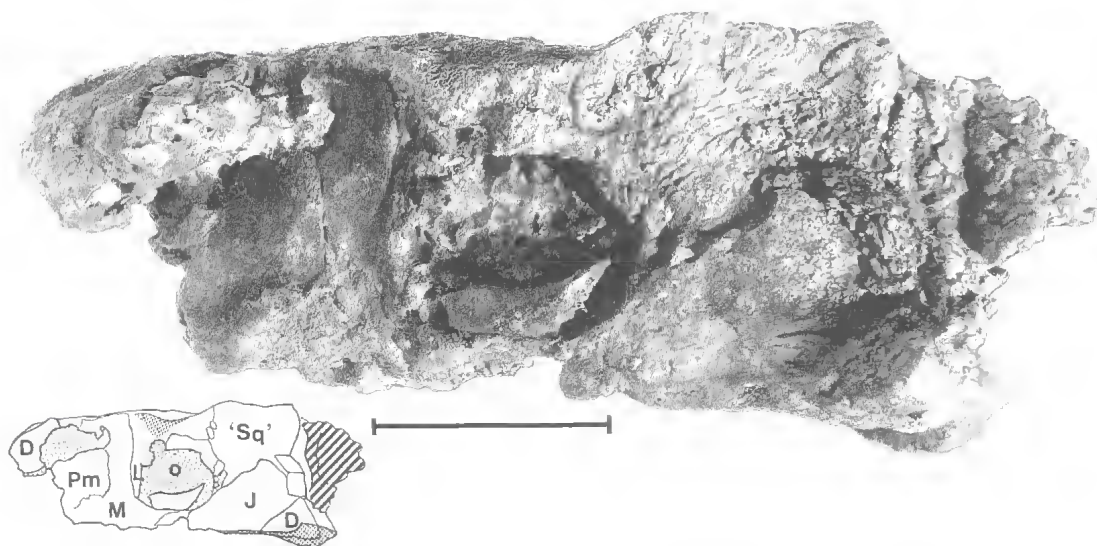


FIG. 7. Skull, in lateral view, of *Minmi* sp. (QM F18101). Anterior is the left. Part of the integumentary dermal armor remains intact behind the skull at right. Inset shows matrix (open dots), broken bone (dots) and still adherent nuchal ossicles (hatching). Scale = 50mm.

known, as all seem to be out of place, some having come to rest inserted between the bases of the large plates and the caudal vertebrae. They may have formed a row along the bottom of the tail, two to every triangular plate.

The appendicular armor is not as completely preserved, however both sets of limbs carried large scutes, as well as small ossicles. The forelimb had a subrounded, keeled scute midway along the humerus and a low, round, pitted scute at the lateral side of the elbow, along the ulna. The hind limb bore a large keeled scute along the back of the calf.

CRANIAL MORPHOLOGY

Although the form of the ankylosaurian skull as a whole is well known, the form of the individual cranial bones is not. Only a single skull (of *Pinacosaurus*) is known showing the contacts between the cranial bones, and those only for the skull roof (Maryanska, 1977). For the rest of the taxa only an isolated maxilla has been described in Galton's (1980) study of *Priodontognathus*. The 'Marathon' specimen, however, shows all of these contacts, except in the braincase where they are fused.

The skull looks like a pentagonal box, because all of the sides (and occipital face) meet the skull

roof at approximately right angles. It is slightly longer (240mm as preserved) than wide (195mm). The skull roof is almost flat, but the nasals arch slightly (c. 3mm) above the level of the skull roof. Unfortunately, the skull has been broken and slightly crushed in places, fortunately, little seems to be missing and the crushing has not done much damage.

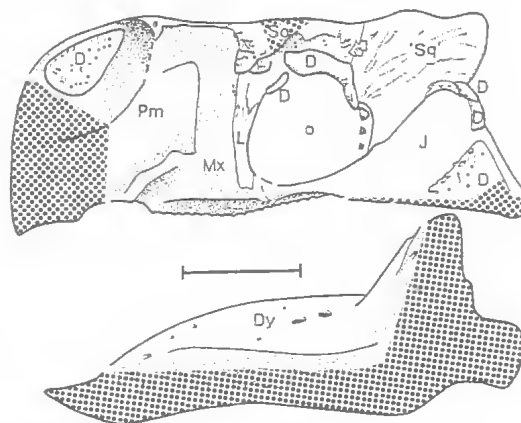


FIG. 8. Reconstruction of skull and left mandible, in lateral view, of *Minmi* sp. (QM F18101). Anterior is to the left. Hatching represents missing parts or broken surfaces. Abbreviations given in text. Scale = 50mm.

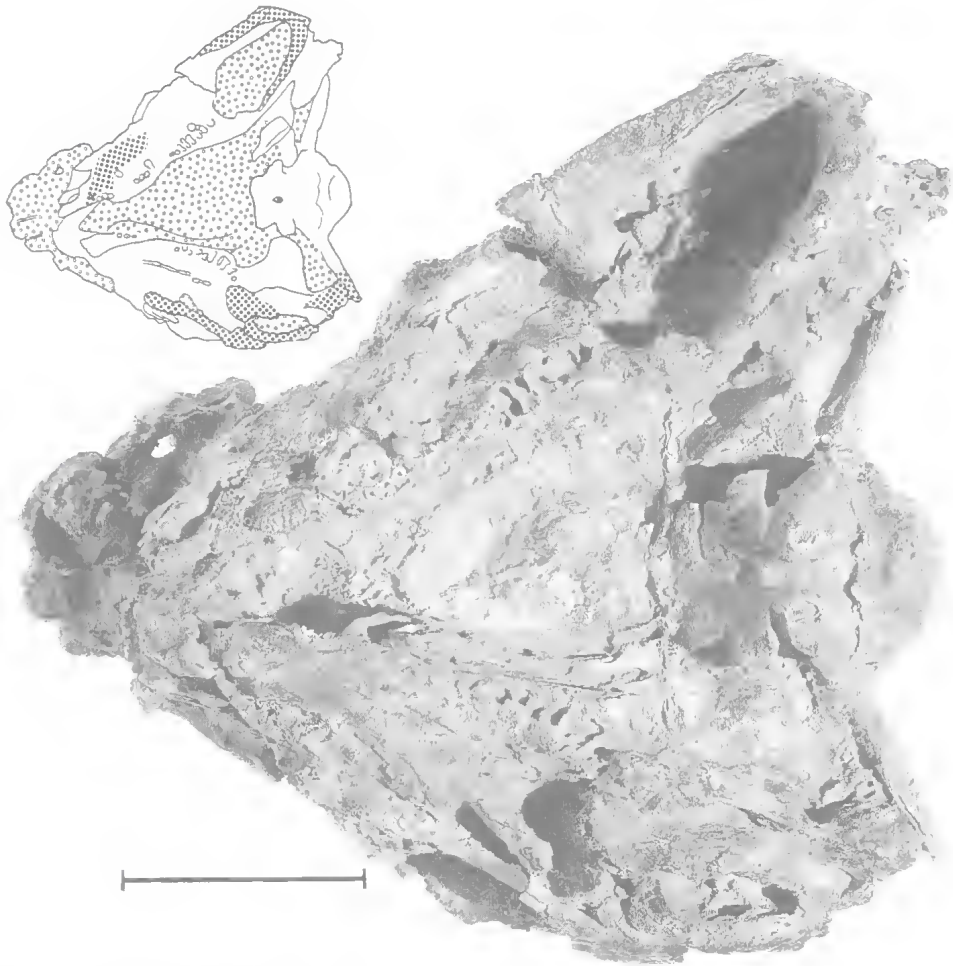


FIG. 9. Skull, in ventral view, of *Minmi* sp. (QM F18101). Anterior is to the left. Inset shows areas still covered by matrix (open dots) and broken bone surfaces (dots). Scale = 50mm.

On the top of the skull both the grooves presumably demarcating the boundaries of the dermal plates and the sutures are clearly preserved (Figs 4, 5). There are also a few dermal ossicles. The skull roof elements are fewer and simpler than in *Pinacosaurus*, basically similar in pattern to those of *Scelidosaurus* (Coombs, Weishampel & Witmer, 1990, fig. 20.1) (Fig. 6). The nasals, prefrontals, frontals, parietals and 'squamosals' and supraorbitals contribute to the dorsal face. The supratemporal fenestrae are entirely obscured by the 'squamosals', parietals and maybe the frontals.

The side of the skull is made up by the premaxilla, maxilla, lachrymal, a little of the supraorbital, and the 'squamosal' and jugal (Figs

7, 8). The orbit is large, laterally directed, and roughly hexagonal in shape. Just in front of it, the sides of the skull converge towards the narial region, forming the abbreviate snout. In the nodosaurid *Edmontonia* the snout (from tip of premaxilla to center of the orbit) comprises about 70% of the total cranial length, but in the ankylosaurid *Euoplocephalus*, and the 'Marathon' skull (as preserved), it is about 60%. The antorbital fenestra has been closed, possibly by a backwards extension of the maxilla. Nor is there any laterotemporal fenestra, which was seemingly covered by the jugal and, maybe, the 'squamosal'. The palate is still largely unprepared, but there is so far no indication of the median vomerine septum, and if it were present

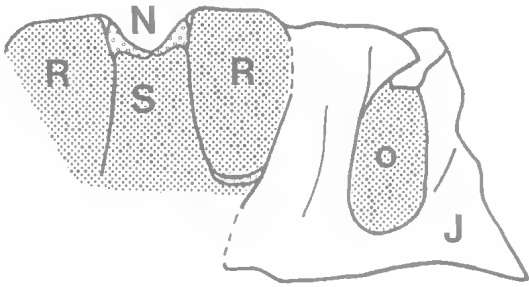


FIG. 10. Diagram of skull, in anterior view, of *Minmi* sp. (QM F18101) showing the the ventral sheets of the nasals. Abbreviations given in text.

and in place, it would expected to have been exposed by now.

A transverse fracture, most obvious on the palatal surface (Fig. 9), crosses the skull through the front of the subtemporal fenestrae. On the left the back of the maxilla and the overlying anterior process of the jugal, have been displaced into the orbital cavity: on the right the subtemporal fenestra seems undamaged, but is occupied by a piece of bone, perhaps part of the coronoid process. Both pterygoids have been broken from their contacts with the basiptyergoid processes and displaced dorsally, more so on the left side. The postorbital region on the left may have been slightly crushed and the right maxilla has been broken and pushed into the palatal vacuity. The left maxillary teeth have all either fallen from their sockets, or been snapped off at the neck, so that a few (four) crowns lie adjacent and lateral to their respective alveoli. The snout is incomplete, but the inferior processes of the premaxillae still associated with the maxillae, suggest that only a little is actually missing, and this is corroborated by the left mandible which is too short to have fitted a much longer skull.

Premaxilla. The premaxilla is represented by a large, smooth plate forming at least 50% of the length of the snout (Fig. 8). This plate seems to be a greatly expanded inferior process of the premaxilla. It overlaps the vertical plate of the maxilla behind, and seemingly rests in a groove in the dorsal margin of the anterior part of the body of the maxilla. The plate is basically flat, but is slightly convex posteriorly and slightly concave dorsally. Its oblique anterodorsal edge presumably forms the posterior margin of the external naris.

Maxilla. The maxilla is a low, broad, elongate element, that forms the ventral margin of the snout and underlies the orbital cavity (Fig. 8). The

body is massive and broad anteriorly becoming thinner but broader posteriorly. A vertical plate rises behind and adjacent to the inferior process of the premaxilla. This plate ascends to the dorsal face of the skull to contact the prefrontal above. In palatal view, the maxillary toothrow is curved, slightly concave laterally. At least 21 alveoli are present, increasing in size posteriorly. The posterior alveoli are transversely broad, but constricted centrally to look like the figure '8'. The medial lobe of the alveolus was (and still is in some) occupied by the root of the replacement tooth, almost as large as that of the functional tooth.

Nasal. The nasals are elongate elements, longitudinally arched (and incomplete) anteriorly but concave transversely, forming a central longitudinal groove. Posteriorly they expand markedly in the transverse plane, giving them a roughly 'T' shape in dorsal view. They meet the frontals in an almost transverse very slightly interdigitating contact, and laterally they are smoothly overlapped by the prefrontals. The anterior moiety medially and posteriorly bounds the external nares. Medial to the nares thin sheets of bone project ventrally at least 35mm from the margins of the nasals, giving the bone an M-shaped form in section (Fig. 10). It is not known how, or if, the passage situated between these sheets contacted the laterally placed chambers.

Prefrontal. The prefrontals are elongate elements, extending anteriorly from the posterior sutural contacts with the frontal and 'squamosal' to the edge of the skull in front of the orbits (Fig. 5). Each joins the supraorbital posterolaterally in a suture, and the vertical plate of the maxilla in front of that in a smooth contact. They are exposed only on the dorsum of the skull.

Lachrymal. The anterior margin of the orbit is composed of a set of unfamiliar, rodlike elements (Fig. 8). The presumed lachrymal is a vertical rodlike element, that extends along this margin. It gradually tapers ventrally, to abut on the maxilla. In addition there are two other rod-like elements, or processes, extending ventrally along the front edge of the orbit, one in anterior to and the other behind the presumed lachrymal. The anterior may be a descending process of the prefrontal or supraorbital, but the possible junction is obscured.

Supraorbital. The subtriangular supraorbital roofs the orbital cavity between the prefrontals and 'squamosals' (Fig. 5). Beneath it posteriorly (on the right side) is an elongate lightly ornamented element (Fig. 8), that appears to be part

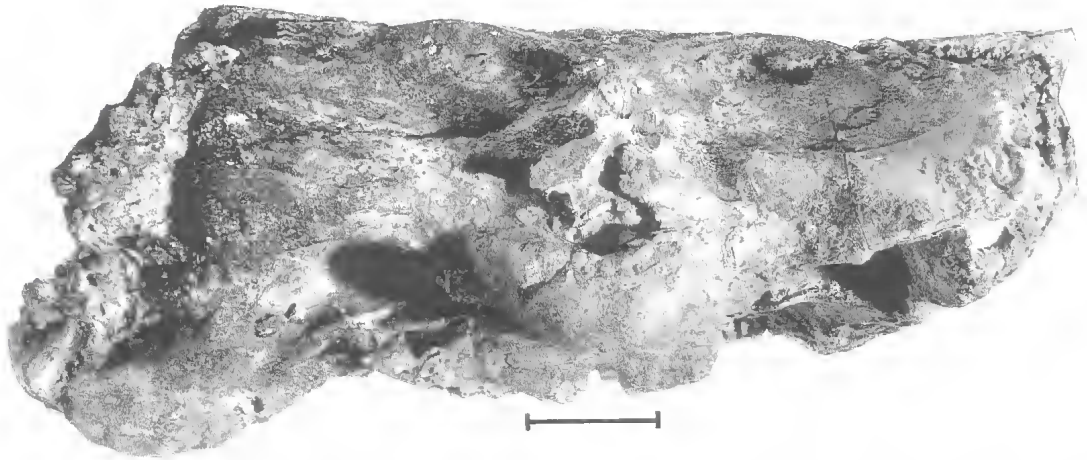


FIG. 11. Skull, in posterior view, of *Minmi* sp. (QM F18101). The upper part of the foramen magnum is occluded, especially on the left, by matrix containing parts of the atlas-axis complex. Also on the left is part of the integumentary dermal armor of the neck, just lateral to the distal end of the left paroccipital process. Scale = 25mm.

of the dermal armor, or perhaps a second supra-orbital.

Frontal. The frontals are fused and basically hexagonal in form, joining the nasals anteriorly, the parietals posteriorly, the prefrontals anterolaterally, and the 'squamosals' posterolaterally (Fig. 5). The dorsal sulcus of the nasals continues posteriorly across the frontals to terminate just anterior to the parietal contact.

Jugal. Behind the maxilla and posteroventral to the orbit is the large, flat, smooth, triangular jugal (Fig. 8). It has the form of two plates, the vertical triangular one behind forming the side of the cheek region of the skull, and a horizontal one in front that floors the orbital cavity. It overlaps the quadratojugal posteriorly — which is thereby obscured from lateral view — and in turn is overlapped by a small, triangular dermal element at its posteroventral extremity.

Squamosal, Postfrontal and Postorbital. The bone here called the 'squamosal' is probably the fused squamosal, postfrontal and postorbital. It is a hexagonal bone, situated at the posterolateral corner of the skull, that forms the upper part of the cheek region (Figs 5, 8). It is overlapped by the jugal below, and sutures to the supraorbital in front and the frontal medially. Unlike the smooth jugal, its lateral face is ornamented by subparallel curved grooves directed posterodorsally, becoming horizontal posteriorly.

Quadratojugal. The quadratojugal is medial to the posterior part of the jugal and lateral to the lower part of the quadrate. It contributed little if

anything to the lateral side of the skull, but is visible along the ventral margin of the jugal arch. In posterior aspect it is revealed as a thin element rising vertically probably to contact the 'squamosal'. A large foramen separates it from the quadrate just above their ventral contact.

Pterygoid. Only the broad, thin horizontal quadrate processes of the pterygoids are so far revealed (Fig. 9). They project laterally from the basisphenoid region where the junctions are broken, to elongate contacts with the quadrates.

Quadrate. Both quadrates are present, but that on the right is obscured. The articular condyles are missing from both. The left is broken at midshaft, but not displaced. The quadrate seems to form a vertical pillar. The lateral inclination of almost 45° of the ventral portion is due to the crushing of the back part of the skull on the left side. The strong, medial vertical plate-like process projects anteromedially, to reach the pterygoids.

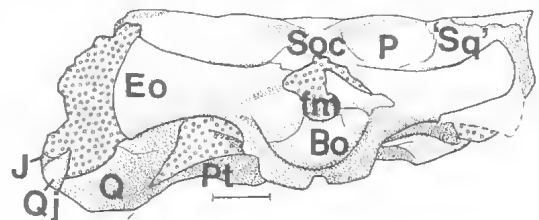


FIG. 12. Skull in posterior view. Abbreviations given in text. Open dots indicates matrix. Scale = 25mm.

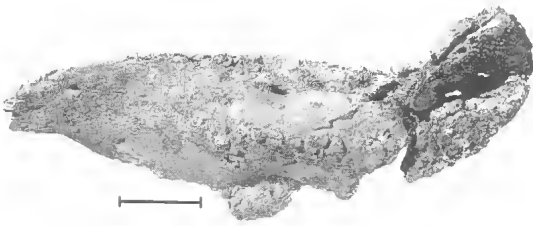


FIG. 13. Mandible (dentary), in lateral view, of *Minmi* sp. (QM F18101). Anterior is to the left. Only the dorsal margin of the body and anterodorsal margin of the coronoid process are preserved, the rest of the edges are breaks. Scale = 25mm.

Parietal. The parietals are transversely elongate elements, fused at the midline, and located along the posterior margin of the skull (Figs 5, 12). Their posterior face seems to extend ventrally for 3cm to contact the paroccipital processes, and overlap the occipital faces of the 'squamosals'.

Exoccipital. The paroccipital processes extend directly laterally and flare at their distal ends, to make up the ventral half of the occipital face of the skull (Fig. 12). From each side a stout pedicle projects ventromedially and a little posteriorly to abut on the basioccipital below the foramen magnum. These exoccipital processes and the basioccipital each contribute about 1/3 to the ventral margin of the foramen magnum.

Supraoccipital. A large supraoccipital in the form of a capital lambda, or inverted 'V', may be present above the foramen magnum (Fig. 12) but further cleaning is necessary to confirm this.

Basioccipital. The occipital condyle, on the basioccipital, sits at the end of a stout, tapering 'neck' that is broader than the condyle itself. In posterior aspect the condyle is reniform and it is directed posteriorly (Fig. 12), rather than posteroventrally.

Basisphenoid. Only the ventral surface of the basisphenoid is yet exposed. Between the basipterygoid processes the ventral face of the basisphenoid is nearly flat, with a small median foramen or depression (Fig. 9). Posteriorly the basisphenoid tubera lie close together near the midline. There is no excavation between and behind them as in certain taxa (*Struthiosaurus*, Pereda-S. & Galton, 1994), but only a smooth surface, facing almost directly backwards, extending to the base of the neck of the occipital condyle. The basioccipital-basisphenoid junction is fused.

Cranial dermal armor. On each side of the skull, roof, three small dermal ossicles sit at the 'apex' of the supraorbital-prefrontal-'squamosal' con-

tact, and a large one sits just lateral to them (Fig. 5). An elongate ossicle sits atop the posterior rim of each 'squamosal'. Dermal ossicles are also found at several places on the sides of the skull, along the posterior margin to the jugal, and the posterior margin of the orbit. A large, elongate ossicle just below the lateral margin of supraorbital, forms the dorsal margin of the orbit. A smaller, triangular ossicle overlies the junction of the lachrymal with the supraorbital. These two may be the second and third supraorbitals, characteristic of thyreophores (Sereno, 1986), although if so they differ from those of the others in that neither is exposed on the top of the skull. A thin, flat, triangular ossicle overlying the posteroventral 'corner' of the jugal (and quadratojugal) is presumably the quadratojugal plate, also found in ankylosaurids.

Dentary. The left mandible is very incomplete as everything medial to the lateral sides of the alveoli has been lost. Only the dentary remains (Fig. 13). But much of its length is preserved, from the down-curved anterior region to well back into the coronoid process. This strong coronoid process arises abruptly lateral to the back of the toothrow, and is clearly more exten-

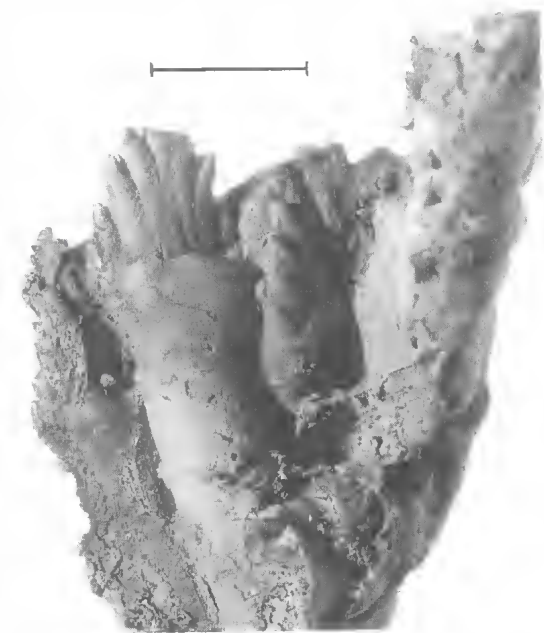


FIG. 14. Three teeth of *Minmi* sp. (QM 18101) as preserved after having fallen from their alveoli. A partially prepared tooth is at the left, two completely prepared teeth at center, and a block of matrix and consolidant at right. Scale = 5mm.

sive than in any other described thyreophore. The distance from the declined anterior part of the toothrow near the front end of the mandible to the coronoid suggests that the mandible was relatively short. *Teeth.* Two sets of isolated teeth are available, one a crown from the anterior part of the skull (presumably the anterior maxilla), and the other a set of three adherent teeth (Fig. 14) from the mid-maxillary (or dentary?) region. The anterior crown has a cingulum 2-3mm deep, with the fluted part of the crown 2-3mm high. The cingulum is broad and bulbous, 3mm wide, and the crown above it only 1mm wide. Seven denticles, and the furrows between them, are present on one side of the crown, whilst the other is almost smooth, with only the lateralmost furrows present. The mid-maxillary teeth are 18-26mm long. The roots are straight and cylindrical, constricted at the neck and open, although perhaps broken, at the tip. The best crown is 7mm high, including a 3mm cingulum. One crown has seven denticles and the remaining two have nine. The enamel is covered with very fine protuberances, giving a finely pebbled appearance under a magnifier. The crowns are 6mm long and 3mm broad at their cingula and 2mm broad just above the cingula. The upper margin of the cingulum is distinct on both faces. Furrows extend all the way from edge to cingulum, unlike the anterior tooth, where they extend only a short distance from the denticles.

VERTEBRAE

So far only the sacrals and middle caudals have been prepared. The sacrals are partially obscured by ossicles that presumably fell onto them from the ventral body wall, so little can be said of them. However it is clear that although the last centrum of the presacral rod was ventrally flattened the

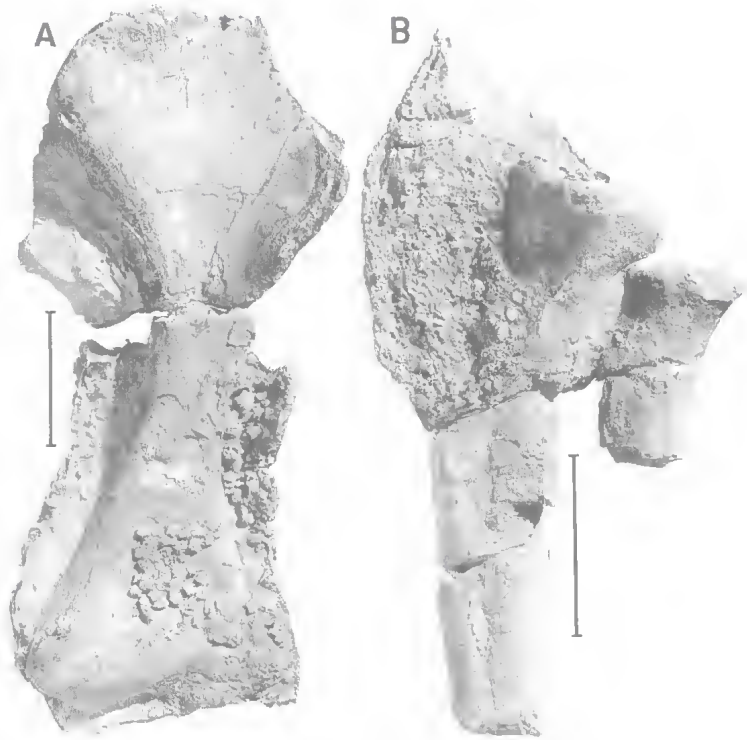


FIG. 15. A, Left humerus, in anterior view, of *Minmi* sp. (QM F18101). Some ossicles adhere to it distally, and the matrix visible along both medial and lateral margins holds a sheet of ossicles in place on its reverse (cf. Fig. 1). B, Proximal segments of left radius and ulna of *Minmi* sp. (QM F18101) in medial view. The block of matrix joining both bones proximally holds dermal armor in place on its reverse (cf. Fig. 1). Scale = 50mm.

synsacral centra lack a ventral sulcus, at least posteriorly.

The more distal of these have a centrum that is hexagonal in section, with a ventral sulcus. The most distal preserved have a broad, flat dorsal surface, with the neural arch restricted to the middle third. Proximally the centra remain hexagonal, but become deeper, and then become quadrangular in section. The ventral sulcus becomes progressively shallower anteriorly, until the ventral face is simply flat. The caudals are slightly amphicoelous.

Although the prezygapophyses are relatively long, they are not as elongate as in ankylosaurids. There is no indication of a tail club, or that the distal part of the tail was modified into a rigid rod. All parts of the tail preserved suggest that some flexibility was possible.

Several series of ossified tendons extend along the tail, mostly above the transverse processes. So they probably were part of the epaxial muscula-

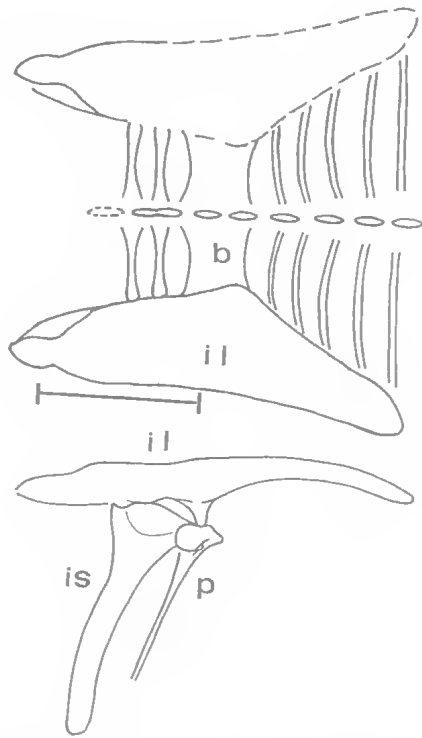


FIG. 16. Reconstructed pelvis of *Minmi* sp.; A, in dorsal view; and B, lateral. In A the dashed line indicates the approximate margin of the left ilium, and the posterior portion of the ilium has been completed from a second specimen, QM F33286. The right side of the reconstructed pelvis is a reflection of the left of the specimen. The broad 'bridge' (b) linking sacrum and ilium may be seen. Scale = 200mm.

ture, although there are one or two that were in the muscles below the transverse processes.

FORELIMB

Scapula. The left scapula is preserved just below the dermal armor. Although preparation is not complete, it shows to have a (mediolaterally) thin blade c. 27cm long, and a well-developed pseudacromial process 3.3cm high. (A complete, but fractured, left coracoid is also present but not yet studied.)

Humerus. The left humerus (26.5cm long) is nearly complete with only the proximolateral 'corner' of the deltopectoral crest missing (Fig. 15A). The shaft is constricted near its midlength and the ends enlarged, but not nearly as strongly as in other thyreophores. The head is anteroposteriorly broadened and set about a third

of the way out from the proximal trochanter. It is supported behind by a buttress extending about a third of the way down the shaft. There is also a ridge along the back of the deltopectoral crest, so forming a shallow fossa between this and the buttress supporting the head. The deltopectoral crest extends about a third of the way down the shaft and lacks the distal expansion described in ankylosaurids (Coombs & Maryanska, 1990).

The distal articular surface, at the elbow, subtends an angle of almost 180° anteroposteriorly. The elbow was probably a hinge joints as in most tetrapods.

Antebrachial elements. The proximal end of the ulna (Fig. 15B) is still incompletely prepared, but it seemingly lacks an olecranal process, so prominent in other thyreophores. Instead there is a flattened, expanded, mushroom-like proximal articular surface that makes an angle of about 45° with the long axis of the shaft. The radial sulcus is well-developed. The shaft is slender and distinctly flattened, with shallow grooves in the broad faces giving an almost figure-8 form to the cross-section.

Little is preserved of the radius (Fig. 15B), although the shaft is slender and oval in cross-section. Both radius and ulna are noticeably more slender than in other thyreophores.

HINDLIMB

Ilium. The ilium is well-preserved on the left side. It is a flat, moderately broad element, with the antacetabular processes inclined laterally at about 35° (Fig. 16A). It is unique among ankylosaurs in that the postacetabular process is elongate. In *Euoplocephalus* the postacetabular process makes up about 27% of the iliac length, while in *Stegosaurus* this is 33%. In the 'Marathon' specimen it is at least 38%. The ilium is connected to the sacrum by a broad 'bridge' of bone. This structure joins the medial margin of the ilium to the dorsal portions of the neural spines of at least three, maybe five, sacrals. These are probably in the middle of the series, although precisely which sacrals cannot be determined until further preparation. The sheet-like 'bridge' seems to overlie the sacral ribs and no trace of it can be seen ventrally although the sacral ribs are prominent. It is well preserved on the right side in QM F18101, but indistinct on the left. It is also present in QM F33286. To my knowledge nothing like this has been reported in other ankylosaurs, but it seems very similar to the sheet

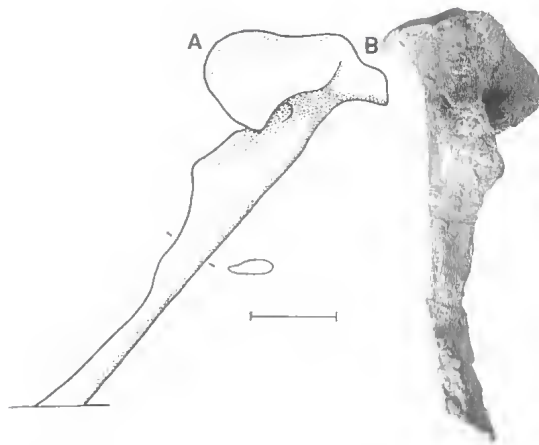


FIG. 17. A, Pubis in lateral; and B, anterior view. Scale = 25mm.

of bone that covers the sacral ribs in *Stegosaurus* (Gilmore, 1914).

Pubis. The left pubis is nicely preserved, although incomplete distally (Figs 16, 17). It has a block-like body, of 'standard' form and a long slender postpubis, that is mildly blade-like in form proximally.

Ischium. The ischium (Figs 16, 18) looks much like those of other ankylosaurs, broad subtriangular proximally and rodlike distally.

Femur. The femur is a robust, straight element, still incompletely prepared. The head is set off medially, as in nodosaurids and the lesser trochanter is not fused to the greater along its length, but is set off by a shallow groove.

Crural & pedal elements. The tibia and fibula are present, the latter at least in part, but have yet to be studied, and no fibulae have been found. Two isolated claw-like unguis resemble those of *Acanthopholis*.

TAPHONOMY

The skeleton was found upside down in a marine deposit. There being no reason to believe this was an amphibious dinosaur, presumably the body washed out to sea. The skeleton was completely articulated — except perhaps for the feet, the distal end of the tail and the axis — and the small dermal ossicles of the back are still largely (or entirely) in place. This suggests that the skin was present and intact on the back right up to the time of burial. No evidence, such as tooth marks, that the carcass was scavenged before it came to lie on the sea floor has been seen, although a few

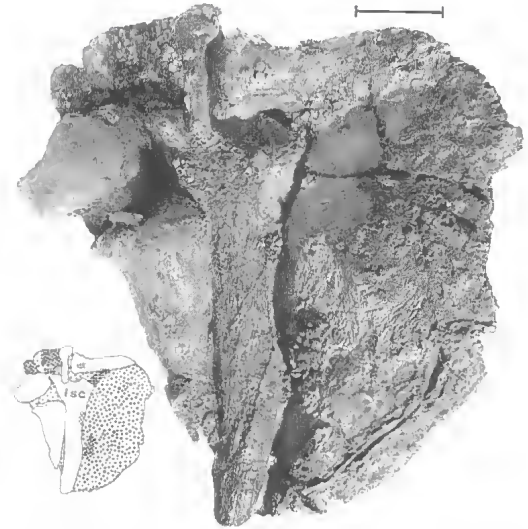


FIG. 18. Lower face of left pelvic block of QMF18101 showing left(?) ischium (lsc) at center. Inset shows matrix indicated by open dots, and blocks of ossicles by dots. Scale = 50mm.

teeth of the small shark *Echinorhinus* were found in association with the skeleton and may indicate that a little scavenging occurred after it sank.

Since the skin of the back seems to have been present, the skeleton may have been held together by it, at least in part. If the skin remained intact, some of the ligaments and capsular tissue might have done so, too. However, the preservation of the left femur still in contact with the acetabulum but directed horizontally outwards, suggests that the ligaments and capsular tissue had relaxed or decayed enough to permit what was presumably a very un-life-like attitude. Furthermore, the discovery of the neural arch of the axis some distance from the skull and neck suggests that this element had become freed of its ligamentous (and bony) attachments. The remaining cervical vertebrae were all found associated or articulated and enclosed within the calcareous nodules, which in turn suggests that the axial neural arch became freed before the nodule started to form.

Either the carcass was more or less complete when it washed out to sea, or it had dried out and mummified. As it was found some distance from the reconstructed shorelines, it had presumably floated for a while before sinking to the bottom. If intact the carcass may have decayed, formed gas bubbles (which would help it float) and eventually ruptured the belly wall, allowing it to sink. Or it may have floated as a dry mummy until it became waterlogged. The ventral sheet of os-

sicles seems to have been disrupted and fallen into the body cavity, consistent with rupture by decay gasses. But the dorsal sheet of ossicles has 'sunk' in between the ribs, which is consistent with mummification, and difficult to explain if that did not occur. Furthermore, the anomalous position of the neural arch of the axis is consistent with this explanation: the carcass had dried out to the extent of allowing it to come free of its attachment to soft tissues and the rest of the skeleton. While the carcass was sinking the arch fell away to come to rest on the seafloor some distance from the remainder of the skeleton. This is not, however, the only possible explanation, it may have been carried off and then dropped by one of the small scavenging sharks.

The evidence seems in favor of the interpretation of mummification prior to being swept out to sea by one point, the 'sinking in' of the dorsal armor and hence the dorsal hide between the ribs. Perhaps this is also consistent with the interpretation of having bloated and burst, but it isn't obvious how. Further work on this aspect is planned as, if true, the mummification interpretation has some interesting implications. First the carcass would have had to have been exposed long enough to dry out, without being noticeably scavenged, and then washed into a river or the sea. This implies an extended, perhaps seasonal, dry period followed by rains heavy enough to remove the carcass, and a surprising lack of scavengers. The seasonality is not inconsistent with what is known about Albian palaeoclimates in Queensland (Dettmann et al., 1992), but perhaps suggests that the seasons were more marked than generally thought.

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